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New recombinations in *Glomeromycota*FRITZ OEHL¹*, GLADSTONE ALVES DA SILVA²,
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ABSTRACT — Combined morphological and molecular biological analyses have achieved major advances in the taxonomy of fungal species in phylum *Glomeromycota*. In this study, we analyzed which species might not yet be attributed to their correct genus, focusing on *Acaulospora myriocarpa*, *A. undulata*, *A. nicolsonii*, and *Scutellospora nodosa*. Based on spore wall structure and phylogenetic support, we recombined the taxa as *Archaeospora myriocarpa*, *Ar. undulata*, *Ambispora nicolsonii*, and *Cetraspora nodosa*.

KEY WORDS — molecular phylogeny, rDNA

Introduction

Combined morphological and molecular phylogenetic analyses have thoroughly changed the classification of the phylum *Glomeromycota* (e.g. Morton & Redecker 2001, Oehl et al. 2008, 2011a). Today, there are three glomeromycotan classes, five orders, 14 families, and 29 genera (Oehl et al. 2011a,d). When species were attributed to these newly established higher taxa, it was known that some species were incorrectly placed due to insufficient available morphological or phylogenetical information (Oehl et al. 2008, 2011a,b,e). In this paper, we consider four of those species — *Acaulospora myriocarpa*, *Ac. undulata*, *Ac. nicolsonii*, and *Scutellospora nodosa*. As a result of new available information, we transfer these species to their proper genera based on their morphological features.

Material & methods

Specimens

Holotype or isotype materials of *Ac. myriocarpa* (OSC, herbarium of Oregon State University, Corvallis, U.S.A.), *Ac. undulata* (OSC), and *Sc. nodosa* (DPP, the Plant Pathology herbarium, Academy of Agriculture, Szczecin, Poland) were analyzed. Type material of *Ac. nicolsonii* (Walker et al. 1984) was either never deposited at OSC or lost during shipping (Richard Halse & Joey Spatafora, curators of OSC, pers. communication); therefore here we rely on the reinterpretation by Walker et al. (1984) of the original species description and illustrations and on comparison of *Ac. nicolsonii* with the type materials of *Ambispora gerdemannii* and *Am. fennica* in Walker et al. (2007).

Morphological analyses

Morphological descriptions of spores (including sporiferous saccules, sporogenous cells, germination shields, and subcellular structures) are based on observations of specimens mounted in polyvinyl alcohol-lactic acid-glycerol (PVLG) and in a mixture of PVLG+Melzer's reagent (Brundrett et al. 1994). Spore structure terminology follows Goto & Maia (2006), Sieverding & Oehl (2006), Oehl et al. (2006), Spain et al. (2006), Palenzuela et al. (2008, 2010, 2011), Goto et al. (2008) and Oehl et al. (2011a–c) for acaulosporoid, ambisporoid, archaeosporoid, entrophosporoid, and gigasporoid spore forming species.

Results

Acaulospora myriocarpa and *Acaulospora undulata*

Both *Ac. myriocarpa* and *Ac. undulata* form bi-walled spores laterally on the neck of a sporiferous saccule. The outer wall is bi-layered and the inner wall triple-layered. The staining reaction of the mycorrhizal structures is faint to absent, and vesicle formation has been observed only infrequently in pure cultures of the two species (Schenck et al. 1986) and then possibly due to misinterpretation (Sieverding own observations). These features attribute both species unequivocally to the genus *Archaeospora* J.B. Morton & D. Redecker emend. Spain (Spain 2003).

Archaeospora myriocarpa (Spain, Sieverd. & N.C. Schenck) Oehl, G.A. Silva, B.T. Goto & Sieverd., **comb. nov.**

MYCOBANK MB 561657

= *Acaulospora myriocarpa* Spain, Sieverd. & N.C. Schenck, Mycotaxon 25: 112. 1986.

Archaeospora undulata (Sieverd.) Sieverd., G.A. Silva, B.T. Goto & Oehl, **comb. nov.**

MYCOBANK MB 561662

= *Acaulospora undulata* Sieverd. Angew. Bot. 62: 373. 1988.

Acaulospora nicolsonii

Acaulospora nicolsonii regularly forms spores on the lateral branch (i.e. pedicel) of a sporiferous saccule. Its spores have three walls: an outer wall, which during degradation shows cracking fissures known only for *Ambispora*

species, a middle wall, and an inner wall. Since the spore morphology exactly matches the features of typical acaulosporoid spores in *Ambispora* C. Walker et al. (= 'acaulo-ambisporoid' spores), we transfer the species to this genus (Spain et al. 2006, Walker et al. 2007, 2008).

Ambispora nicolsonii (C. Walker, L.E. Reed & F.E. Sanders) Oehl, G.A. Silva, B.T. Goto & Sieverd., **comb. nov.**

MYCOBANK MB 561663

= *Acaulospora nicolsonii* C. Walker, L.E. Reed & F.E. Sanders,
Trans Br. Mycol. Soc. 83: 360. 1984.

Scutellospora nodosa

New observations on the germination shield of the type material of *Sc. nodosa* reveal that the shields are hyaline and multiply lobed, which is typical for *Racocetraceae* species (e.g. Oehl et al. 2010). Since the species has triple-walled spores (Błaszkowski 1991, Oehl et al. 2008), we transfer it to the genus *Cetraspora* Oehl et al. (*Racocetraceae*).

Cetraspora nodosa (Błaszk.) Oehl, G.A. Silva, B.T. Goto & Sieverd., **comb. nov.**

MYCOBANK MB 561664

= *Scutellospora nodosa* Błaszk., Mycologia 83: 537. 1991.

Discussion

Archaeospora has now three species— two with smooth spore walls (*Ar. trappei*, *Ar. myriocarpa*) and one with an ornamented (undulating) spore surface (*Ar. undulata*).

Ambispora has now three species (*Am. callosa*, *Am. fecundispora*, *Am. leptoticha*) for which only glomoid spore formation is known and two species (*Am. jimmerdemannii*, *Am. nicolsonii*) for which only acaulosporoid spore formation is known. All other *Ambispora* species have spore bimorphism (*Am. appendicula*, *Am. brasiliensis*, *Am. fennica*, *Am. gerdemannii*, *Am. granatensis*) (Spain et al. 2006, Walker 2008, Goto et al. 2008, Palenzuela et al. 2011).

Three major characteristics strongly support transfer of *Ac. nicolsonii* to *Ambispora*: i) the presence of three walls (outer, middle, inner), ii) the clear pedicel on the sporiferous saccule neck, referred to as a 'stalk' in the protologue (Walker et al. 1984), and iii) outer spore walls that have the typical 'cracking fissures' as known for outer walls of almost all known *Ambispora* species, e.g. *Am. appendicula*, *Am. gerdemannii*, *Am. fennica*, and *Am. brasiliensis* (see illustrations in Walker et al. 1984; Spain et al. 2006, Goto et al. 2008). The absence of fracturing (i.e., 'plate-like splitting') of the middle wall layers in *Am. nicolsonii* (Walker et al. 2007) might be the most important morphological difference between it and *Am. gerdemannii* and *Am. fennica*, while the outer walls in both *Am. nicolsonii* and *Am. gerdemannii* do not stain in Melzer's reagent but do in *Am. fennica* (Walker et al. 2007; Oehl, pers. observation).

The recent transfer of *Am. brasiliensis* to *Acaulospora* by Krüger et al. (2011) cannot be accepted; the spore morphology of the Scottish material described and illustrated as *Acaulospora brasiliensis* by Krüger et al. (2011) does not match the morphology of *Am. brasiliensis*, and their sequenced material apparently represents a true *Acaulospora* species rather than authentic *Am. brasiliensis*. Krüger et al. (2011) unfortunately ignored the major characters elaborated by Spain et al. (2006) for *Ambispora* species and detailed by Goto et al. (2008) for *Am. brasiliensis*.

There have been doubts about the shield morphology of *Cetraspora nodosa* (*Scutellospora nodosa* in Oehl et al. 2008), and sequences of the fungus deposited in public databases during more than 10 years were apparently misidentified. New combined morphological and molecular phylogenetic analyses, based on identified sequences recently placed in the public databases, now show a congruency between morphological and molecular data supporting *C. nodosa* as closely related to *C. helvetica*, *C. pellucida*, and *C. gilmorei* (Oehl et al. 2010, 2011b) within the monophyletic genus *Cetraspora*.

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